High growth and microzooplankton-grazing loss rates for phytoplankton populations from the Mississippi River plume region

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Abstract

During the July/August 1990 NECOP cruise, taxon-specific growth, and microzooplankon grazing and sedimentation loss rates were measured on dominant phytoplankton populations in the plume/hypoxia region. Taxon-specific growth rates (μ) ranged from <0.1 to >3.0 d^{-1} with highest rates (>2 d^{-1}) in the plume region. Many surface growth rates in the plume were close to or exceeded previously published μ_{max} values. For most taxa, including diatoms and non-diatoms, growth rates decreased in the hypoxia region. Significant microzooplankton grazing loss rates were noted only for small phytoplankton (< 15 μm); rates for these taxa were high (>1.0 d^{-1}) in the plume region and decreased in the hypoxia region. Sedimentation was an important loss only for a few diatoms. Our data suggest that during the summer in the plume region phytoplankton production rates are high and most of this production is recyled within the surface layer.

Anthropogenic nutrient inputs from the Mississippi River may produce enhanced primary productivity in the northern Gulf of Mexico (Riley 1937; Thomas and Simmons 1960; Sklar and Turner 1981; Turner and Rabalais 1991). However, the dynamics and heterogeneous nature of the Mississippi River plume have complicated attempts to relate changes in levels of riverine nutrient inputs to corresponding changes in regional production and phytoplankton growth (Thomas and Simmons 1960; Sklar and Turner 1981; Lohrenz *et al.* 1990). Furthermore, significant questions still remain regarding the nutrient(s) controlling primary production in this region (Schiller and Boyle 1987; Dortch and Whitledge 1991; J. Ammerman, pers. comm.). Phytoplankton dynamics within this region are also poorly understood.

Because of the complexities of this region and because rate processes occur at the species-level, we proposed to examine the growth, sedimentation and microzooplankton grazing loss rates of dominant individual species in the Mississippi River Plume/Inner Gulf Shelf region as part of the the NECOP program. In this paper, we present our preliminary data from the first NECOP cruise conducted in July/August 1990 in order to (1) compare taxon-specific ^{14}C-autoradiography and dilution estimates of growth, and (2) provide estimates of sedimentation and microzooplankton grazing loss rates.

Methods

Sampling was conducted at three stations during the July/August 1990 NECOP cruise aboard the RV *BALDRIDGE*. These three stations followed a transect from the river mouth at Southwest Pass to the inner part of the hypoxia region (Fig. 1). The first two stations, which will be referred to as plume stations, were sampled on July 22 and July 25; the third station, which will be referred to as the hypoxia station, was sampled on August 2-3.

All water samples were collected early in the morning, generally before dawn, with modified acid-washed Niskin bottles and a nylon rope. In order to avoid chemical contamination, all rubber parts of the Niskin bottle (o-rings, closure tubing, etc.) were replaced with silicone parts. Collected water was immediately transferred to 20-L polyethylene carboys for sample processing.

A Sea-Cat CTD with transmissometer and PAR sensor was used to measure vertical profiles of temperature, conductivity, PAR, and percent light transmission. Inorganic carbon concentrations were determined by infrared absorption spectroscopy.

The ^{14}C technique was used for estimating carbon uptake. Experiments were performed on July 22, July 25 and August 2. Briefly, 1-L polycarbonate bottles were gently filled with raw water, inoculated with

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$NaH^{14}CO_3$, and incubated in a deck-simulated in situ incubator (Lohrenz *et al.* 1990). Samples from 0.5m, 3m and 6m were incubated at 50 percent, 12 percent and 3 percent of surface irradiance using neutral density screens. Incubations started near dawn and terminated at dusk (15- to 16-hour incubation) or the following dawn (24-hour incubation). Following incubation, aliquots from the sample bottles were preserved with Lugol's solution, immediately filtered onto 0.22 μm Millipore filters, and transferred onto gelatin-coated slides. These gelatin-coated slides were then frozen for track autoradiographic analysis.

Track autoradiography was used to estimate the specific activity (dpm $cell^{-1}$) of individual cells (Carney and Fahnenstiel 1987). Gelatin-coated slides were dipped in filtered subbing solution (Knoechel and Kalff 1976) and then dipped in NTB-3 photographic emulsion at 29°C. Slides were allowed to dry and then were developed as described in Carney and Fahnenstiel (1987). Tracks per cell were enumerated and activity (dpm $cell^{-1}$) was calculated (Knoechel and Kalff 1976). For this paper only 50 to 80 cells were counted for each taxa; therefore, these results should be viewed as preliminary.

We estimated taxon-specific growth rates from ^{14}C-autoradiography experiments by making simple assumptions about cell growth. The approach is first order and it is described in various ways throughout the literature (e.g., Welschmeyer and Lorenzen (1984), Li (1984), and Li and Goldman (1986)). Let C^* = specific activity of cellular ^{14}C (dpm $cell^{-1}$), U = uptake rate of C (C $cell^{-1}$ d^{-1}), t = time (d), μ = growth rate (d^{-1}), and α = isotope discrimination factor. Then the instantaneous time rate of change of cellular C^{14} is

$$\frac{dC^*}{dt} = \alpha U - \mu C^*. \quad (1)$$

Note that when growth is referenced to a cellular framework it represents a loss term reflecting the transfer of carbon due to cell division. At time t = 0, the initial value of C^* is 0. The solution of (1) is

$$C^* = \frac{\alpha U}{\mu}(1-e^{-\mu t}). \quad (2)$$

Equation 2 is further simplified by recognizing that

$$C_{asy} = \frac{\alpha U}{\mu} \quad (3)$$

where C_{asy} is the asymptotic activity of C^* and moreover

$$C_{asy} = C_m C_c \quad (4)$$

with C_m = activity of the inorganic medium, which for all practical purposes remains approximately constant throughout the experiment and C_c = cell carbon content. Thus C^* can be related to μ at any time t by parameters that can be directly measured (C^*, t, and C_m) or by approximating C_c through estimates of cell volume.

$$C^* = C_{asy}(1-e^{-\mu t}) \quad (5)$$

Finally, the growth rate μ is calculated from (5) and

$$\mu = -\frac{1}{\Delta t} \ln \frac{C_{asy}-C^*}{C_{asy}} \quad (6)$$

where, Δt is the incubation time interval corresponding to C^*. All of the ^{14}C-growth rates reported herein were calculated according to (6) and will be referred to as ^{14}C-autoradiography growth rates.

The dilution method also provided another independent estimate of phytoplankton growth as well as an estimate of the grazing loss rate by the microzooplankton community (Landry and Hassett, 1982). In these experiments microzooplankton abundances were manipulated through a series of dilutions with filtered seawater, and changes in abundances of phytoplankton populations were noted. These bottle dilutions were performed by mixing appropriate volumes of prescreened seawater (<200 μm) with filtered seawater (GF/F filtered water) in 2-L polycarbonate bottles. Bottles were incubated for 24h in a temperature controlled deck incubator. Because increasing bottle dilution alleviates grazing pressure, the slope of phytoplankton growth rate (dependent variable) across dilution treatments (independent variable) is an estimate of the microzooplankton grazing loss rate, and the intercept is an estimate of the phytoplankton growth rate. These dilution experiments were done either simultaneous (July 25) or a day later (August 3) than the ^{14}C experiments.

Phytoplankton sedimentation rates were determined from enumeration of a preserved phytoplankton sample collected from a free-floating MULTITRAP design sediment trap (Knauer *et al.*, 1979; Knauer *et al.*, 1990). These traps were deployed at 15m for a period of 1-2 days on July 25 and August 2.

In all cases, phytoplankton samples were preserved with Lugol's solution. These samples were then stored in amber vials until phytoplankton preparations were made. These phytoplankton samples were then either filtered onto slides and cleared (Dozier and Richerson, 1975) or settled onto coverslips. Phytoplankton were enumerated under low magnification (200-300X) and high magnification (600-1200X). A minimum of 1000 cells were enumerated. Phytoplankton volumes were estimated by determining the average cell dimensions from a a minimum of 30 randomly chosen individuals of each taxon from each sampling date. Because only 30 individual were measured, these volume estimates should be regarded as preliminary. The average dimensions were then applied to the geometric configuration which best approximated the shape of the taxon (e.g. spheres, prolate spheres). These cell volumes were then converted to carbon concentrations using the conversions of Strathman (1967) for diatoms and non-diatoms.

Results

Ambient conditions — Environmental conditions at the three stations suggest that we did sample along the plume/shelf gradient. The surface mixed layer was relatively shallow (< 4m) at stations 1 and 2 and surface salinity, nitrate, and temperature values were approxi-

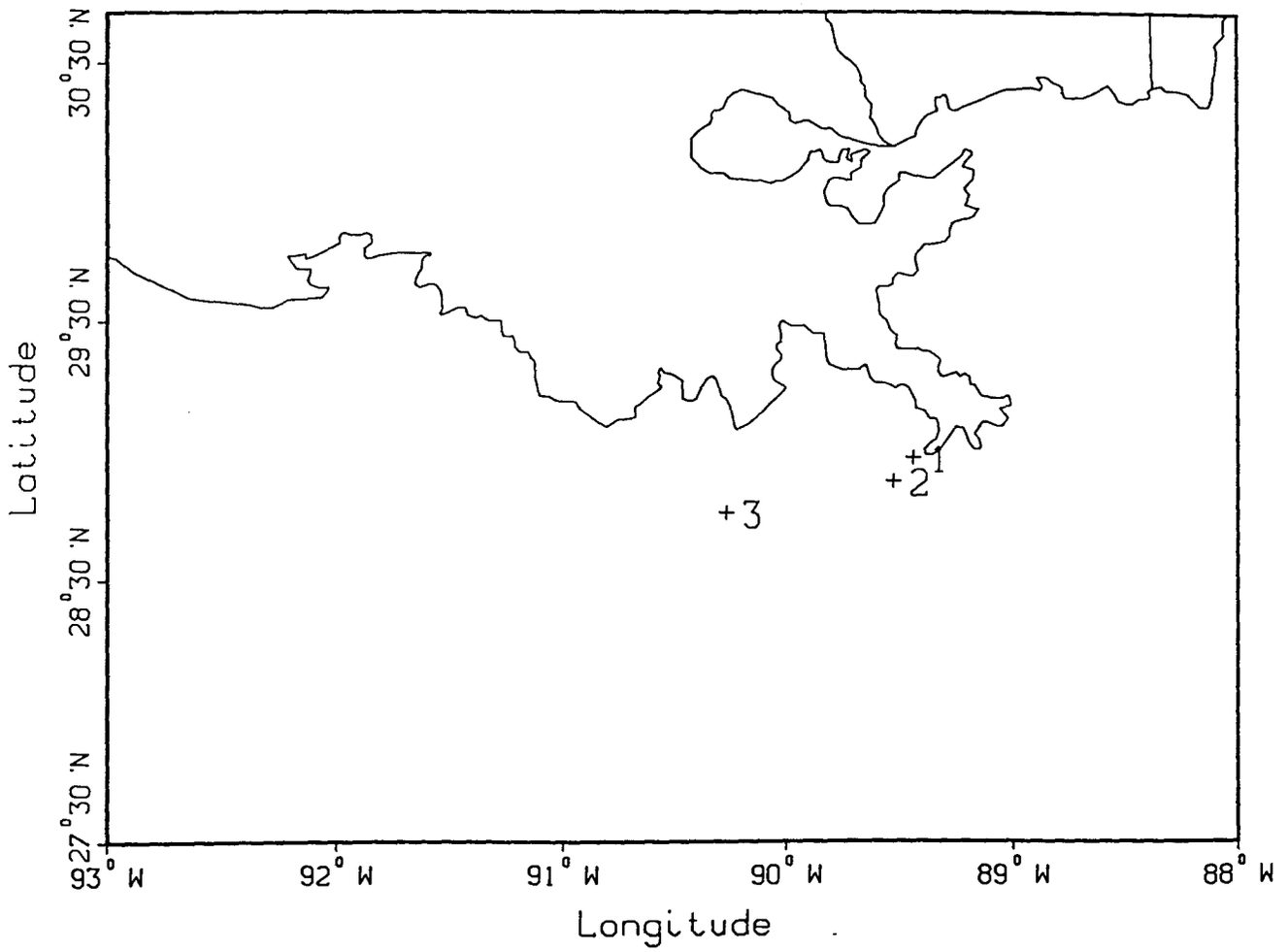

Fig. 1. Location of sampling stations (+) during the July/August 1990 NECOP Cruise. The two plume stations, 1 and 2, were sampled on July 22 and 25, respectively. The hypoxia station (3) was sampled on August 2-3.

Table 1. List of abundant taxa from surface waters on July 25 and August 2-3 and inventory of rate process data for these taxa. Abundances (cells ml^{-1}) are listed in order from most abundant on each date and rate process estimates were made where indicated (x).

Date	Taxa	Abundance	C-14 G[1]	Dil. G[2]	MG[3]	Sed[4]
July 25	*Cyclotella caspia*	1191	X	X	X	X
	Rhodomonas spp.	891	X	X	X	X
	Skeletonema costatum	766	X	X	X	X
	Small monads (e.g. *Ochr.*)	544	X			
	Gymnodinium sp. large	197				
	Cryptomonas sp.	165				
	Katodinium rotunda	147	X	X	X	X
	Cyclotella striata	41	X	X	X	X
	Total phytoplankton abundance	4047				
Aug. 2-3	Small monads (e.g. *Ochr.*)	1523	X	X	X	X
	Rhizosolenia fragilissima	676	X	X	X	X
	Rhodomonas spp.	429	X	X	X	X
	Nitzschia pungens	387	X	X	X	X
	Cerataulina pelagica	352	X	X	X	X
	Cymnodinium sp.-small	94	X	X	X	X
	Total phytoplankton abundance 3605					

[1] ^{14}C-autoradiography growth rate
[2] Dilution growth rate
[3] Microzooplankton grazing loss rate
[4] Sedimentation loss rate

Table 2. Growth (^{14}C-autorad. and dilution), microzooplankton grazing and sedimentation losses rates (d^{-1}) of representative taxa from the July/August 1990 NECOP Cruise.

Date	Taxa	Z (m)	^{14}C-auto.	Dil. Growth	Micro. Graz.	Sed
July 22	*Skeletonema cost.*	0.5	2.1	—	—	—
		5.0	0.2	—	—	—
July 25	*Skeletonema cost.*	0.5	1.0	1.7	0.3*	—
		3.0	0.5	—	—	—
		6.0	0.1	—	—	—
		0-15				0.3
July 25	*Cyclotella caspia*	0.5	3.0	2.5	0.6	—
		0-15				0.03
Aug. 2-3	*Nitzschia pungens*	0.5	0.6	0.9	0.2*	—
		3.0	0.3	—	—	—
		6.0	0.2	—	—	—
		0-15				<0.01
Aug. 2-3	*Rhizosolenia frag.*	0.5	0.4	0.6	0.4*	—
		3.0	0.3	—	—	—
		6.0	0.1	—	—	—
		0-15				<0.001
July 25	*Ochromonas* sp.	0.5	2.2	—	—	—
		3.0	2.8	—	—	—
		6.0	0.5	—	—	—
Aug. 2-3	*Ochromonas* sp.	0.5	1.6	1.0	1.0	—
		3.0	0.8	—	—	—
		6.0	0.1	—	—	—
		0-15				<0.001
July 25	*Katodinium rot.*	0.5	2.4	2.4	1.5	—
		3.0	2.1	—	—	—
		6.0	0.2	—	—	—
		0-15				<0.001
Aug. 2-3	*Gymnodinium* sp.-small	0.5	1.1	0.5	0.4	—
		3.0	0.3	—	—	—
		6.0	0.1	—	—	—
		0-15				<0.001
July 25	*Rhodomonas lac.*	0.5	2.7	2.0	1.4	—
		3.0	1.0	—	—	—
		6.0	0.1	—	—	—
		0-15				0.01
Aug. 2-3	*Rhodomonas lac.*	0.5	1.0	1.6	1.5	—
		3.0	0.5	—	—	—
		6.0	0.1	—	—	—
		0-15				<0.001

mately 15-18 ppt, >25 μM l^{-1}, and 29-30°C, respectively. These two stations will be referred to as plume stations. Conversely, station 3 was located in the hypoxia region of the inner shelf and environmental conditions were markedly different than those reported for stations 1 and 2. The surface-mixed layer was approximately 5 m and salinity and nitrate concentrations in this layer were 26 ppt and <3 μM l^{-1}, respectively. Surface temperature was 31°C.

Growth and loss rates — Growth rates were determined for at least 13 of the most abundant taxa on the three dates sampled (Table 1). Because of the overwhelming dominance of *Skeletonema costatum* on July 22, growth rates were determined for only two taxa, *Skeletonema* and *Cyclotella*. However, on July 25 and August 2-3 growth rate estimates were determined for at least six of the more abundant taxa.

At the three stations, surface growth rates varied from 0.2 to >3.0 d^{-1}. There was a general pattern of decreasing growth rates with greater distance from the river mouth; mean surface growth rates for diatoms and non-diatoms were higher on July 25 than on August 2-3. The mean diatom growth rate decreased from 1.6 d^{-1} on July 25 to 0.5 d^{-1} on August 2-3 whereas the non-diatoms decreased from 2.3 d^{-1} to 1.2 d^{-1}. Most taxa exhibited very high surface-growth rates (> 2 d^{-1}).

on July 25 including some diatoms, dinoflagellates, cryptophytes and other small flagellates (Table 2). Growth rates generally decreased with depth; rates at the 1percent light level (ca. 5-7 m) were generally 0.1-0.2 d^{-1} (Table 2). Thus, euphotic zone average growth rates are much lower than the high near-surface values.

Although there were some differences among taxa, overall surface ^{14}C autoradiography growth rates were not significantly different from dilution growth rates ($p > 0.25$, $n = 14$; Table 2). Likewise, comparisons on the individual dates also were not significantly different (July 25, $p > 0.5$, $n = 6$, August 2-3, $p > 0.3$, $n = 8$). Thus, ^{14}C and dilution techniques provide similar estimates of growth.

Microzooplankton grazing was a major loss for phytoplankton in the plume and hypoxia region (Table 2). Smaller phytoplankton (<15 μm) exhibited higher grazing loss rates than larger organisms. The mean microzooplankton grazing loss rate for small cells, e.g. *Rhodomonas* spp., *Ochromonas* sp., small monads, *Katodinium rotunda*, and *Gymnodinium* sp.-small (*Cyclotella* spp. included on July 25), was 1.0 d^{-1} (range 0.6-1.5 d^{-1}) on both dates. The mean growth rates for these same taxa on the same dates were 2.2 d^{-1} and 1.4 d^{-1}, respectively. Because the growth and loss rates were both measured in the surface-mixed layer they are comparable. However, in contrast, the microzooplankton grazing loss rates for larger phytoplankton, *Skeletonema costatum*, *Nitzschia pungens*, *Rhizosolenia fragilissima*, *Cerataulina pelagica*, and *Gymnodinium* sp-large, were never significantly different from zero.

Unlike microzooplankton grazing loss rates which were measured in the upper 1 m of the water column, sedimentation loss rates were an integrative measure over the upper 15 m. In this case, they are not directly comparable to surface growth and grazing loss rates because of the strong gradients that existed in the water column; however, they are useful for examining the relative role of sedimentation. With the exception of several diatoms, *Skeletonema costatum*, *Cyclotella caspia* and *C. striata*, all sedimentation loss rates were <0.01 d^{-1}.

Discussion

The growth rates measured in the plume region (stations 1 and 2) are some of the highest growth rates reported for marine phytoplankton assemblages (Furnas, 1990). Furthermore, despite limited comparative data, many of our taxon-specific growth rates (Table 2) are the highest reported for a given species under field conditions and/or are close to or exceed the maximum reported growth rate (μ_{max}) for the species under optimal culture conditions. For example, *Katodinium rotunda* has a μ_{max} of 1.5 d^{-1} at 20°C (Throndsen, 1976) and has a maximum reported field growth rate of 1.0 d^{-1} (Owens *et al.*, 1977). Our growth rate for *Katodinium rotunda* of 2.4 d^{-1} in the surface waters on July 25 exceeds both of the previous values (Table 2). Likewise, *Skeletonema costatum* has a carbon-specific μ_{max} of 1.7 d^{-1} at 25°C (Langdon, 1988). Maximum reported field growth rates for *Skeletonema costatum* were as high as 4.0 d^{-1} (Furnas, 1982), but carbon-specific values would be much lower and probably around 2.5 d^{-1} (Langdon, 1988). In this study the highest growth rate for *Skeletonema costatum* was 2.1 d^{-1} (Table 2).

The good agreement that we found between surface ^{14}C-autoradiography and dilution growth rate estimates ($p > 0.25$) supports our high growth rate estimates. Rarely in the past have species-specific growth rates been measured with two independent techniques (Furnas, 1990). Because neither technique actually measures growth or cell division, this type of collaboration is needed and should be more common in future studies.

The exceptionally high growth rates found in this study should be of little surprise given the environmental conditions present in the surface waters of the Mississippi River Plume during the summer. Water temperatures were approximately 30 °C and ambient dissolved nitrate concentrations exceeded 90 μM l^{-1} on July 22 and 25 μM l^{-1} on July 25. Thus, given the high temperatures and saturating light levels (50 percent of I_o) of a near surface incubation, it is not surprising that many species were growing at/near μ_{max}.

Silica may occasionally be an important limiting nutrient in the Mississippi plume region (Dortch and Whitledge, 1991) and our preliminary growth rate data can be used to assess the degree of silica limitation during our study. Clearly, silica or any other nutrient were not severely limiting growth in the surface waters at our plume stations (stations 1 and 2) where diatom growth rates were high and close to μ_{max}. In the hypoxia region (station 3), however, there is the potential for strong nutrient limitation as growth rates decreased (Table 2). But, the decrease in growth was found for both diatoms and non-diatoms suggesting that the limiting nutrient was not silica. The growth rate decrease for diatoms was greater than for non-diatoms, but because the composition of the diatom community also changed along this gradient, it is difficult to interpret these subtle shifts in growth rate without direct comparisons of relative growth rates for the same species. Further evidence for the lack of strong silica limitation can be found in the dissolved nutrient ratios at these stations. Silica:nitrogen ratios of <1 have been used to indicate possible silica limitation (Dortch and Whitledge, 1991). In the surface waters at the three stations, Si:N ratios varied from approximately 1-6, suggesting that silica was not strongly limiting diatom production.

Our data cannot be used to rule out the possibility of silica limitation for some diatom species nor does it suggest that silica is unimportant in this region. Because diatom composition does change as we move to the hypoxia region, differential silica limitation (competition for silica) among diatoms may be an important process. At this point, we simply have too little data to evaluate the role of silica. However, because

silica is a good indicator of eutrophication (Schelske *et al.*, 1986), it is important to determine its role, both presently and historically.

One major objective of the NECOP program was to determine the fate of phytoplankton carbon in this region. Our data suggests that much of the surface algal production appears to be recycled within the surface-mixed layer. For many species, particularly small phytoflagellates, microzooplankton-grazing loss rates in the surface waters were comparable to growth rates. Microzooplankton-grazing was not a major process affecting populations of large diatoms (Table 2). These results are consistent with the role of micrograzers in other environments (Fenchel, 1988).

Although it is difficult to compare sedimentation loss rates quantitatively with other processes in this study because sedimentation rates were measured at 15 m, sedimentation only appears to be an important fate for one diatom, *Skeletonema costatum*, and possibly two others *Cyclotella caspia*, and *C. striata*. Sedimentation rates were extremely low for all other taxa, including small flagellates and some large diatoms (*Rhizosolenia fragilissima, Cerataulina pelagica*).

When considering the significance of our results to the broad objectives of the NECOP Program, it should be remembered that these preliminary measurements have many spatial inconsistencies which prevent us from thoroughly evaluating the importance of growth and loss processes. Microzooplankton grazing rate measurements were confined to the upper 1 m as were the greatest density of growth rate measurements. On the other hand, sedimentation rates were determined at 15 m where no other processes were measured. In the Mississippi River Plume the surface-mixed layer is very shallow and strong environment and growth gradients exist within the water column. Mean euphotic zone or water column growth rates would be much lower than surface rates and the factor(s) controlling phytoplankton growth and dynamics below the upper 1 m of the surface-mixed layer are poorly understood. Future studies should include measurements on the same spatial scale and more intensive vertical rate process measurements.

To summarize, in the plume region during the July/August NECOP cruise surface phytoplankton growth rates for most taxa were high (>2 d^{-1}) and much of this growth was recycled within the surface-layer by microzooplankton grazing. In the hypoxia region growth rates were lower, but still most of this carbon was recycled within the surface-layer by microzooplankton grazing. Sedimentation was only an important loss for several diatoms.

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